STATISTICAL ANALYSIS OF ECOLOGICAL DIVERSITY

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Contents

Summary

The problem of defining and measuring ecological diversity by means of well-behaved indexes is considered. Any diversity measure is a function of the species abundances in the community, which are usually unknown quantities. Accordingly, the abundances are estimated on the basis of suitable sampling strategies which are able to handle the problems arising when working with ecological communities as well as ensuring good statistical properties. Subsequently, the abundance estimates are used to make inference about diversity on the whole community. Emphasis is laid particularly on the problem of comparing diversity among several communities. Finally, some field applications for analyzing diversity in animal and plant communities are surveyed.

1. Introduction

The concept of *diversity* arises quite naturally in various subject areas. Intuitively, diversity is related to the apportionment of some quantities into a number of well-defined categories, which may take the form of resources, investment, time, energy, abundance, etc, according to the problem under study (Patil and Taille, 1979*a*).

In an ecological framework, the diversity concept relies on the apportionment of abundances (or some related quantities such as biomass or coverage) into a number of animal or plant categories forming the ecological community under study. In this contest, it is however of basic importance to define the term *community* as all the organisms in a delineated study area belonging to the taxonomic group of interest (Pielou, 1977, p.269). Indeed, it would be unfeasible to consider every living form in the area, from molecules and genes to species. For example, the comparison of apportionment of tree numbers and nematode numbers would be absurd without some importance weighting. Thus, the considerable problem to be faced when analyzing diversity would be how to define weights. On the basis of what criteria may nematodes or trees be considered more important? In this case, dealing with diversity may sound like an oxymoron. Accordingly, a taxonomic group at a higher level than species (e.g. families, classes, etc) is usually chosen and the *ecological* diversity refers to all members of the group within the community under study, which are usually known as a *taxocene*. Thus, for forest stand communities, for example, all plants or tree species in an area may represent the taxocene subjected to diversity analysis, while for animal communities, the taxocene may be the snakes in a stretch of a tropical forest.

The primary aim of scientific analysis on ecological diversity is to formally define the concept of diversity and subsequently quantify diversity by means of suitable indexes. In this context, statistical analysis is involved only from a descriptive point of view. However, any diversity measure depends on the apportionment of abundances among species, usually referred to as *relative abundances*. Obviously, these quantities may only be known by performing a complete survey of the community over the whole study area, which is not feasible in most real situations. Thus, at this stage the problem lies in estimating abundances on the basis of sample surveys. To this purpose, it is necessary to choose the sampling design for performing the survey. This choice must be made not only on the basis of theoretical considerations, but also on the basis of practical considerations regarding field conditions and the nature of the biological community under study. Subsequently, the abundance estimates may be used to estimate diversity indexes and to assess hypotheses regarding the diversity of the whole communities. A very important aspect of this inferential procedure is the ordering of ecological communities with respect to diversity.

In accordance with these considerations, in Section 2 some formal definitions of ecological diversity are presented and the more common indexes for measuring diversity are reviewed. Then, in Section 3, some suitable designs for sampling ecological communities (which are usually without-frame populations) are considered in order to estimate abundances. Subsequently, in Section 4, some parametric and nonparametric estimators of diversity indexes are described together with the procedures for assessing hypotheses on the corresponding population indexes. Finally, Section 5 is devoted to the particular problem of ordering communities according to their diversity while Section 6 contains some practical applications of diversity analysis in animal and plant communities.

2. Defining and measuring ecological diversity.

As pointed out by Patil and Taille (1979*a*), a formal definition of diversity as a concept and its measurement have long been lacking. The simplest method for measuring diversity is to merely count the number of species present, usually referred to as *species richness*. However, more precise measurement may be obtained by taking into account how the individuals are apportioned into species. Within the framework of mathematical information theory, Pielou (see *e.g.* Pielou, 1977) was one of the first to attempt rigorous measurement of ecological diversity as the level of *uncertainty* in the community. Indeed, if an individual is selected from the community, it is quite obvious that as population diversity increases (in an intuitive sense), so does the uncertainty about which species it belongs to. Accordingly, it may seem reasonable to equate diversity with uncertainty and to use the same measure for both.

2.1 Shannon index

In the framework of mathematical information theory, Shannon and Weaver (1949) and subsequently Khinchin (1957) establish three conditions that any index is required to meet as an appropriate measure of uncertainty. Suppose an ecological community of N individuals partitioned into S categories (species) and denote by N_l the abundance of *l*-th category $(l = 1,...,S)$, where $N = N_1 + ... + N_S$. Moreover, denote by $p_l = N_l / N$, the relative abundance of the *l*-th category, where $p_1 + ... + p_S = 1$. Thus, any uncertainty or diversity index is defined as a function $H(p_1,..., p_S)$ that meets the following conditions:

i) $H(p_1,..., p_S)$ takes its maximum when $p_l = 1/ S (l = 1,...S)$;
ii) the diversity index is unchanged if there are m other categories with no individual, that is

$$H(p_1,..., p_S, 0,..., 0) = H(p_1,..., p_S)$$

iii) under an additional classification that divides the community into T categories with relative abundance $q_h (h = 1,...R)$, the diversity index related to the double classification that divides the community into SR categories with relative abundances π_{lh} turns out to be

$$H(\pi_{11},...,\pi_{SR}) = H(p_1,..., p_S) + \sum_{l=1}^{S} p_l H(q_{1/l},..., q_{R/l})$$

$$= H(q_1,...,q_R) + \sum_{h=1}^{R} q_h H(p_{1/h},...,p_{S/h}) \qquad (1)$$

where $q_{h/l} = \pi_{lh} / p_l$ and $H(q_{1/l},...,q_{R/l})$ represents the diversity index induced by the second classification within the $l-$th category of the first one, while $p_{l/h} = \pi_{lh} / q_h$ and $H(p_{l/h},...,p_{S/h})$ represents the diversity index induced by the first classification within the $h-$th category of the second one.

From a practical point of view, condition *i*) ensures that in a community of S categories the diversity will be maximum when all the categories are present in equal proportions. Indeed, it is at once apparent that a community in which the categories are quite evenly represented has high diversity, while, if there are few categories with large abundances and the remaining are poorly represented, the diversity is lower. As to condition *ii*), it simply ensures that, given two communities in which categories are evenly represented, the community with the larger number of categories has the higher diversity. Finally, condition *iii*) implies that if the two classification criteria are completely independent, then $\pi_{lh} = p_l q_h$, in such a way that (1) reduces to

$$H(\pi_{11},...,\pi_{SR}) = H(p_1,...,p_S) + H(q_1,...,q_R),$$

i.e. the increase in diversity induced by the two-way classification is simply the sum of the diversity due to any single classification. On the other hand, if the classification criteria are completely equivalent, thus giving rise to the same $S = R$ categories, then $H(\pi_{11},...,\pi_{SR}) = H(p_1,...,p_S) = H(q_1,...,q_R)$, i.e. the second terms of (1) vanish and no increase in diversity takes place. Practically speaking, condition *iii*) ensures that the increase in diversity due to a two-way classification depends on the level of concordance between the two criteria of classifications.

It can be shown (see *e.g*. Pielou,1977, Chapter 19) that the only function of relative abundances satisfying conditions *i*)-*iii*) is proportional to the quantity

$$\Delta_{Sh} = -\sum_{l=1}^{S} p_l \ln p_l \qquad (2)$$

which is known as the *Shannon index*. It is at once apparent that Δ_{Sh} ranges from 0 , when all the individuals belong to the same category, to $\ln S$, when $p_l = 1/S$, *i.e*. the categories are evenly apportioned.

A more direct derivation of (2) is offered by Brillouin (1962) again within the framework of information theory. Suppose a message is composed by using a total of N symbols of which N_1 are of the first kind, ..., N_S are of the S-th kind. Since the number of possible messages formed is $N!/(N_1!...N_S!)$, the amount of uncertainty prior to receiving the message may be measured by any increasing function of this quantity. Accordingly, the author proposes using the quantity

$$B = \frac{1}{N} \ln \frac{N!}{N_1!...N_S!}$$

which is usually referred to as the *Brillouin index*. However, it can be proven that, as the N_l's increase, by using the approximation $\ln x! = x(\ln x - 1)$ for the factorials involved, B reduces to Δ_{Sh} (see *e.g.* Pielou, 1977, p.300).

It is worth noting that the Shannon index is the only one with the appealing property that if the community under study is subdivided in any way, then the diversity index can be subdivided into additive components according to (1). This makes it possible to take into account the hierarchical nature of biological classification such as when, for example, an ecological community is classified first according to genera, and within each genus the individuals are subsequently classified according to species. In this case the Shannon index of total diversity is nicely split into two components: genus diversity and species diversity within a genus (Pielou, 1977, p.303). Moreover, if a community is classified twice, *e.g.* taxonomically and by habitat, the Shannon index may be alternatively split into species diversity plus habitat diversity within the species or into habitat diversity plus species diversity within habitat (Pielou, 1977, p.305).

2.2 Alternative Diversity Indexes

Despite the popularity of the Shannon index and its appealing properties, many other diversity indexes have been proposed in literature. The best known of these is the *Simpson index*, which was not originally proposed to measure diversity but rather the related and converse aspect of the dominance of a few species in the community (Simpson, 1949). The index is based on the quantity $N_l(N_l - 1)/\{N(N-1)\}$ which represents the proportion of couples of individuals belonging to *l*-th species with respect to all the possible couples of individuals in the population. If this proportion is great for a given species, it is quite obvious to conclude that the community exhibits a high degree of concentration. Thus, since as community size increases these proportions converge to p_l^2 for any l, one concentration index might turn out to be

$$C = \sum_{l=1}^{S} p_l^2 \ .$$

Obviously, since measures concentration, any decreasing function of C constitutes a diversity index. Pielou (1977) suggests using

$$\Delta_{Si} = -\ln \sum_{l=1}^{S} p_l^2 \qquad (3)$$

which shares the property of ranging from 0 to $\ln S$ with the Shannon index. Alternatively, the quantity

$$\Delta_{Si} = 1 - \sum_{l=1}^{S} p_l^2 \tag{4}$$

which ranges from 0 to $(S-1)/S$, is more usually referred to as the Simpson index.

A compromise between these two major indexes has been elegantly proposed by Renyi (1970) within the framework of information theory applied to statistical physics. If condition *iii*) is relaxed in favour of a less restrictive one in which the diversity induced by two independent classifications is the sum of the diversity due to any single classification, then the only indexes satisfying these conditions are proportional to the quantities

$$\Delta_\alpha = \frac{1}{1-\alpha} \ln \sum_{l=1}^{S} p_l^\alpha \quad , \alpha \in \mathbb{R} .$$

It is at once apparent that Δ_α reduces to the Shannon index for $\alpha = 1$ and to the Simpson index of type (3) for $\alpha = 2$. Another well-known family of diversity indexes related to the Shannon and Simpson indexes is the Good family (Good, 1953)

$$\Delta_{\alpha,\beta} = \sum_{l=1}^{S} p_l^\alpha (-\ln p_l)^\beta , \quad \alpha, \beta > 0 ,$$

which reduces to the Shannon index for $\alpha = \beta = 1$. Baczowski *et al.* (1998) further generalize Good's family by allowing $(\alpha, \beta) \in \mathbb{R}^2$ and determining the range of (α, β) values for which $\Delta_{\alpha,\beta}$ satisfies conditions *i*) and *ii*). Note that for $\alpha \geq 1$ and $\beta \leq 0$, $\Delta_{\alpha,\beta}$ actually constitutes a dominance index. For example, when $\alpha = 2$ and $\beta = 0$, $\Delta_{\alpha,\beta}$ reduces to one minus the Simpson index of type (4).

2.3 Average Rarity Diversity Indexes

A very effective approach for measuring diversity is offered by Patil and Taille (1979*a*) on the basis of the intuition that a community is diverse when there is a large number of rare species. Accordingly, the authors propose measuring the rarity of each category by suitable numerical quantities and adopting the average community rarity as a diversity index. Thus, if $R(l)$ is the rarity of the *l*-th category, the diversity index turns out to be

$$\Delta = \sum_{l=1}^{S} p_l R(l) , \tag{5}$$

which actually represents the average species rarity in the community. Now, the problem lies in defining a rarity measure for each species. Obviously, since it may be useful that (5) equals 0 in presence of a single-species community, any rarity measure must be such that it satisfies this constraint. In this framework, two broad classes of diversity indexes may be identified according to the rarity measure adopted. A *dichotomous-type rarity measure* is obtained when the rarity of the *l*-th species depends only on its relative abundance, *i.e.* $R(l) = R(p_l)$. In this case (5) reduces to

$$\Delta = \sum_{l=1}^{S} p_l R(p_l)\,. \qquad (6)$$

On the other hand, a *rank-type rarity measure* is obtained when the rarity of the *l*-th species depends only on the rank of its relative abundance, *i.e.* $R(l) = R\{r(l)\}$ where $r(l)$ represents the rank of p_l in the sequence $p_{(1)} \le \ldots \le p_{(S)}$ of relative abundances ranged in descending order. In this case (5) reduces to

$$\Delta = \sum_{l=1}^{S} p_{(l)} R\{r(l)\}\,. \qquad (7)$$

If a dichotomous rarity measure of type $R(l) = (1 - p_l^{\beta})/\beta$ is used in (6), the well known Δ_β family is obtained, where

$$\Delta_\beta = \frac{1 - \sum_{l=1}^{S} p_l^{\beta+1}}{\beta}\,. \qquad (8)$$

Note that Δ_β is defined for any $\beta \in \mathbb{R}$ and the diversity profile obtained by plotting Δ_β versus β is decreasing and convex. However, Patil and Taille (1979*a*) suggest the parameter restriction $\beta > -1$ in order to obtain certain desirable properties for the indexes. Moreover, Δ_β reduces to $S - 1$ for $\beta = -1$, while it reduces to the Shannon index for $\beta = 0$ and to the Simpson index of type (4) for $\beta = 1$.

If a rank-type rarity measure of type $R(l) = 1$ if $l > m$ and $R(l) = 0$ if $l \le m$ is used in (6), the *right-tail sum family* of diversity indexes is obtained, where

$$T_m = p_{(m+1)} + \ldots p_{(S)}, \qquad m = 0, 1, \ldots, S \qquad (9)$$

represents the relative abundance of the $S - m$ rarest species. Obviously $T_0 = 1$ and $T_m = 0$. Also in this case, the plotting of T_m versus m joining the successively plotted points gives rise to the *right-tail sum diversity profile* which turns out to be convex and decreasing from 1 to 0.

Patil and Taille (1979*a*) point out the importance of diversity profiles and emphasize that since diversity is actually a multidimensional concept, any scalar diversity index may not be appropriate to measure alone the various aspects of diversity. Moreover, the right-tail sum diversity profile plays a fundamental role in the issue of diversity ordering (see *Ecological diversity ordering*).

2.4 Species-Abundance curves

Another way to approach the measurement of diversity is on the basis of the species-abundance relationship (see *e.g*. Pielou,1977). Instead of listing the number of individuals for each species in the community, it is possible to list the number of species, say S_1 represented by one individual,..., the number of species, say S_K, represented by K individuals, where K denotes the abundance of the most abundant species and $S_1 + ... + S_K = S$. Accordingly, the sequence of relative frequencies $f_r = S_r / S$ $(r = 1,...,K)$ constitutes a frequency distribution for the number of individuals per species which is usually referred to as the *species-abundance curve*. Obviously, the shape of this frequency distribution gives some insight into the diversity of the community under study. For example, if the frequency distribution decreases monotonically, then the rarest species are more frequent than the abundant ones, so that diversity should be high. Usually, a mathematical model is supposed for f_r, in such a way that the parameters of the model may be adopted as diversity indexes. Even if the number of individuals per species is actually a discrete quantity ranging from 0 to K, the more widely applied models assign a frequency f_r for all the positive natural numbers $r = 1, 2, ...$

Among the frequency models for describing the species-abundance curve, Pielou (1977) focuses on the use of the *zero-truncated negative binomial* model

$$f_r = \frac{\Gamma(\kappa + r)}{r!\Gamma(\kappa)} \frac{p^r (1-p)^\kappa}{1-(1-p)^\kappa}, r = 1, 2, ...; \ 0 < p < 1; \kappa > 0 \qquad (10)$$

where κ may be interpreted as a diversity index. Indeed, when $\kappa \le 1$, the one-individual species are the most numerous while for $\kappa > 1$ species with intermediate abundance are more common than rare species (see *Model-based inference*). As $\kappa \to 0$, the zero-truncated negative binomial model reduces to the *logarithmic series* model

$$f_r = \frac{-p^r}{r \ln(1-p)}, \ r = 1, 2, ... \qquad (11)$$

which is suitable in the presence of a very large number of rare species, where the rarity is more and more marked as p approaches zero.

2.5 Related issues

Finally it must be noticed that a large body of literature is devoted to quantifying some aspects related to diversity, such as *evenness* or *equitability* and *dominance* or *concentration*. Many articles on these subjects are contained in the volume edited by Grassle *et al*. (1979)

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